Diversity of Feeding Mechanisms among Embryos of Pacific Northwest *Thais*

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(3 Text figures)

INTRODUCTION

PROSOBRANCH EMBRYOS MAY HATCH as veligers or may metamorphose in the capsule. These developmental strategies are associated with different types of embryonic food supply. The free-swimming veligers collect a variety of nanno- and microplanktonic cells with cilia on the velar edge and pass them to the mouth along the distinct food groove; algal cells 4 μm to 30 μm in diameter are the most frequently captured foods (FRETTER & MONTGOMERY, 1968). Embryos that do not feed in the plankton are provided with a large yolk supply, either within each egg, or externally, in the form of sterile "nurse eggs."

Embryos provided with nurse eggs must consume several of these "particles," each as large as the embryo itself, when the feeding begins, and each an order of magnitude larger (range 130 - 325 μm, FIORONI, 1966) than the typical foods of a free-swimming counterpart, to obtain its yolk. Such a task requires feeding mechanisms not possessed by the free-swimming larvae.

Three mechanisms have been described from observations on Muricacea. Eggs are swallowed whole by *Murex senegalensis* Gmelin, 1791, *M. quadrifrons* Lamarck, 1822, *M. incarnatus* (Röding, 1798), *Thais emarginata* (Deshayes, 1839), *T. hippocastaneum* (Lamarck), and *T. dubia* (Krauss) (KNUDSEN, 1950; GOHAR & EISAWY, 1966; LEBOEUF, 1971; and BOKENHEIM & NEUGEBAUER, 1938). The ingested eggs are visible as distinct bulges in the body wall, and will spill out intact from an embryo opened during the feeding period. The nurse eggs of *T. emarginata, T. hippocastaneum,* and *M. senegalensis* clump to form a mat. Those of *T. lapillus* (Linnaeus, 1758) also clump, but fall to pieces in the process, so the embryos consume only pieces of eggs (THORSON, 1946; PELSENEER, 1916). In the most different feeding method, a *Murex virgineus* Sowerby embryo manipulates a nurse egg with its velar lobes, collapses the egg by pressing on it with the lobes, and then sucks up the contents (NATARAJAN, 1957).

FEEDING OF *Thais* EMBRYOS

The 4 Pacific Northwest species of *Thais* belong to the subgenus *Nucella,* and have many morphological and ecological features in common. Individuals form dense populations in the intertidal zone, where all feed readily on *Balanus glandula* Darwin, 1854 (SPIGHT, 1972, and observations of R. T. Paine on *T. lima* (Gmelin, 1791) in the laboratory). Females attach their tough-walled egg capsules to intertidal rock surfaces; these open after 3 to 5 months and between 10 and 50 hatchlings emerge from each (the number varies with the capsule size, but in the same way for the 4 species; SPIGHT, *op. cit.*). Despite the many characteristics common to these species, the embryos use 3 different means to obtain their yolk supplies.

A freshly deposited *Thais emarginata* capsule contains a few fertile eggs and many infertile nurse eggs. EMLEN (1966) counted 300 to 1000 eggs (mean, 615; SD = 221) in capsules from Port Townsend, Washington. LEBOEUF (1971) counted 64 to 750 (mean about 500) eggs in others from California; of these 3 to 39 (mean, 16) developed.

The larvae begin ingesting the nurse eggs when the velar lobes are partially expanded (Figure 1). The nurse eggs are usually matted together when the embryos are feeding. The embryos grasp eggs on the outside of the mass and often cannot be detached without injury. The mouth, esophagus, and body expand to enclose the eggs as they are pushed down the digestive tract by the long cilia lining it. As each egg is swallowed, the body outline becomes more irregular, and often each embryo in a capsule has a unique shape (Figure 1). Embryos must be

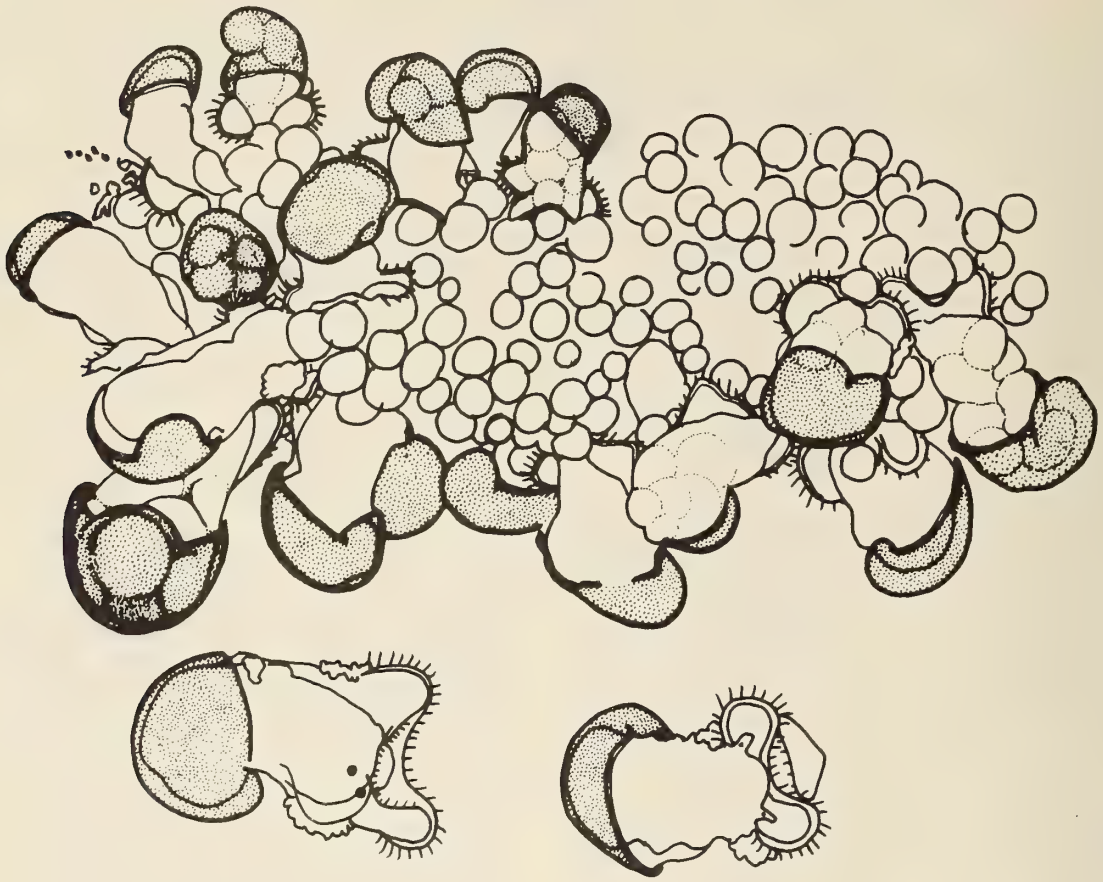

Figure 1

A matted mass of *Thais emarginata* nurse eggs removed from a capsule, with attached month-old veligers (two of the larger ones have fallen off the mass). The outlines of whole eggs can be seen through the transparent body wall of several veligers. The 4.2 mm long mass is from a capsule collected near Friday Harbor, Washington.

capable of feeding on intact nurse eggs for only a few days, since eggs not eaten at this time (*e. g.* when there are only 3 or 4 embryos in the capsule) will remain in the capsule until the end of the developmental period.

Thais canaliculata (Duclos, 1832) capsules may also contain nurse eggs. HOUSTON (1971) counted between 200 and 300 eggs in freshly deposited capsules from California; 97% of these were nurse eggs. Capsules about the same size (1 cm long) collected on San Juan Island, Washington, contained about a tenth as many eggs, and most of these were fertile (the mean egg count in samples taken at the beginning and the end of the developmental period did not decrease significantly; SPIGHT, 1972). However, the single San Juan Island female that has oviposited in the laboratory placed infertile eggs in all of the 18 capsules we opened, and among 5 capsules with prefeeding veligers, 16% to 92% of the eggs were developing.

The feeding method of the *Thais canaliculata* embryos was unique. An embryo grasped a nurse egg with the cilia in the dense patches on the front of the head and the propodium (Figure 2) and rotated it until pieces flaked off. The infertile eggs did not clump.

Infertile *Thais lamellosa* (Gmelin, 1791) eggs are rare. The embryos (Figure 3) have neither the expansible mouth and esophagus, nor the very large cilia lining mouth and esophagus or head and propodium, used by the other species for manipulating and ingesting nurse eggs. The few infertile eggs remain intact in the capsule through the developmental period, and are unavailable to the embryos (we assume they will be broken apart with the radula just prior to hatching).

Thais lima females maintained in a 10° C cold room by R. T. Paine deposited a few capsules in the fall of 1971. All of the eggs in the capsules opened were developing. The embryos were not examined in detail.

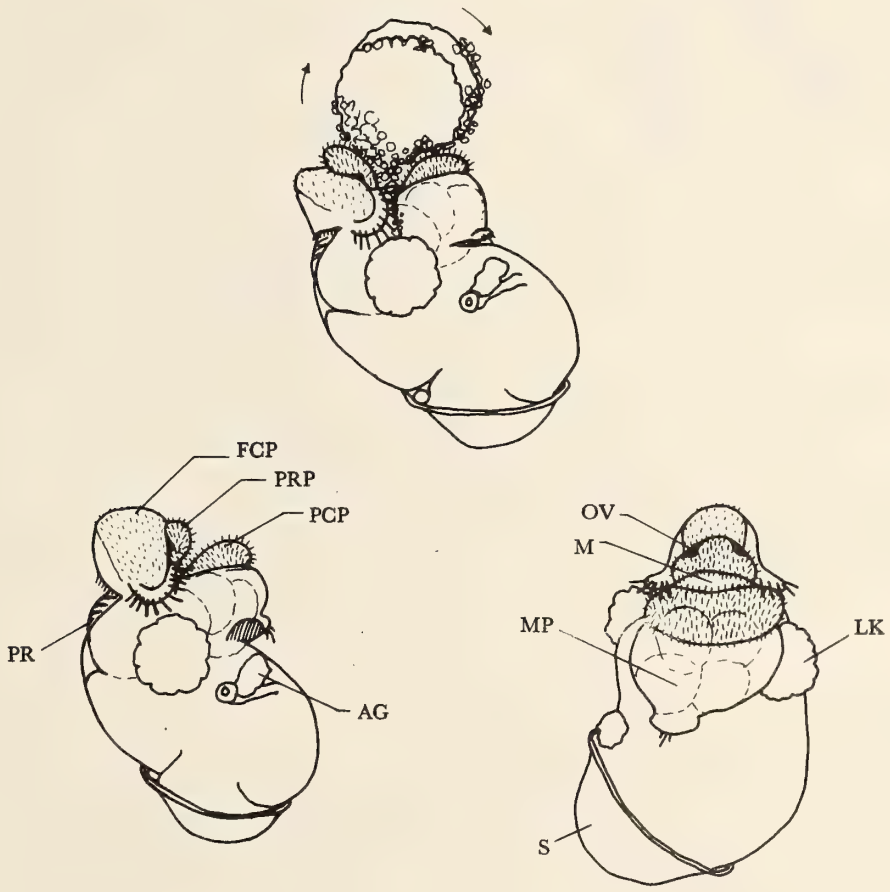

Figure 2

A *Thais canaliculata* veliger feeding on an infertile egg. The front of the head (PRP, preoral ciliary patch) and propodium of the foot (PCP, propodial ciliary patch) were heavily ciliated. The veliger rotated the egg over the mouth with these cilia until pieces of the egg were torn off. This veliger was removed from a capsule 31 days after it was deposited in an aquarium with running seawater (temperature 12° C). The velar lobes are not as expanded as those of *Thais emarginata* or *Thais lamellosa* veligers of the same age.

AG – anal gland; FCP – frontal ciliary patch; LK – larval kidney; M – mouth; MP – metapodium; OV – optic vesicle; PR – larval heart; S – shell

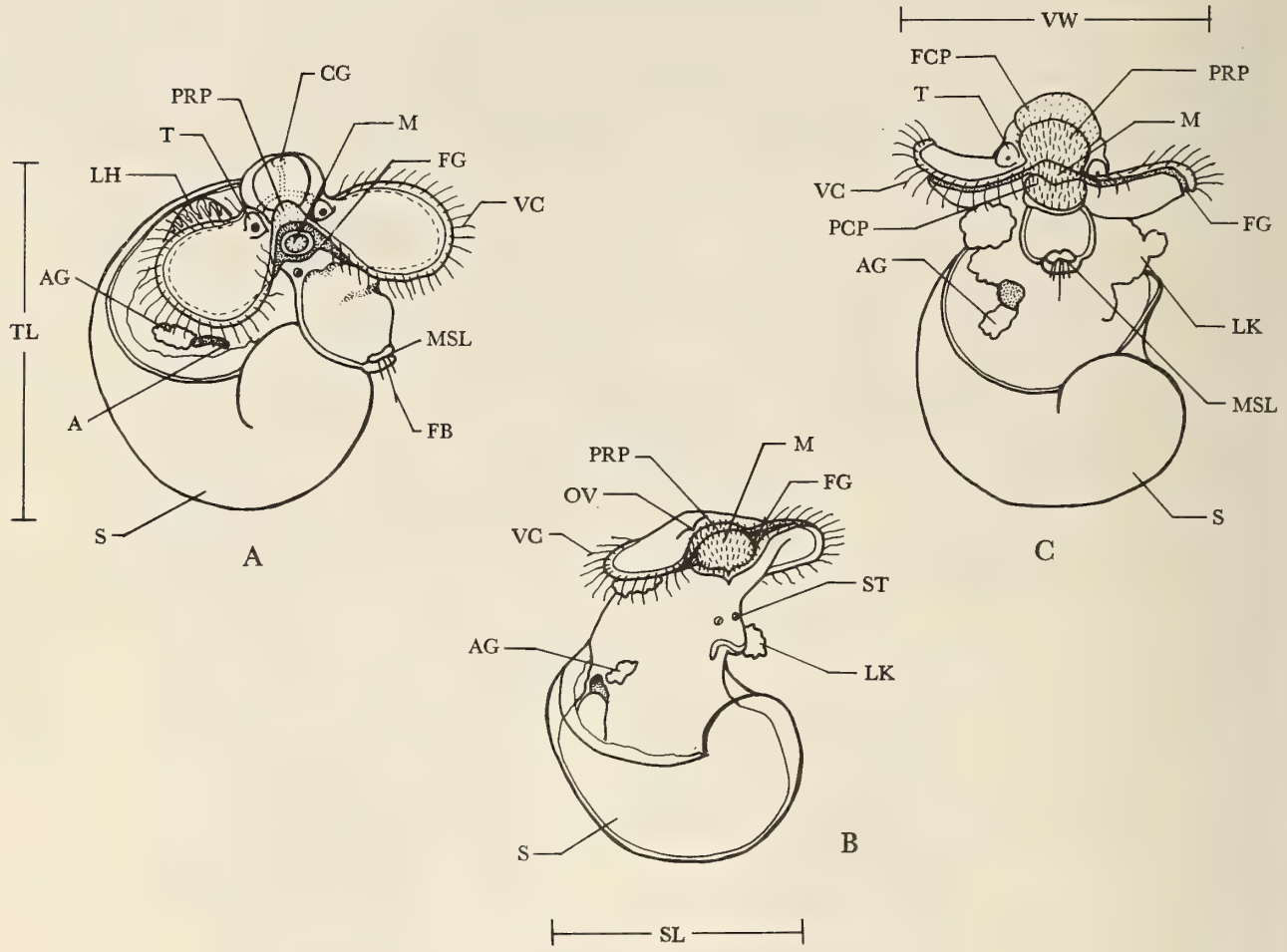

Figure 3

Month-old embryos of three Northeast Pacific *Thais* species. Capsules were deposited in aquaria with running seawater on 3 May by *Thais emarginata* (B) and *Thais canaliculata* (C) females, and on 5 May by *Thais lamellosa* (A) females; all were opened on 10 June. Temperature 12° C. The VELAR LOBES are flat from the sides of the head, and joined by the pre-oral ciliary patch (PRP), which is prominent in C. The vela of C are fleshier and inflatable. The head area of B is flat; the velar lobes rest on thick stalks, so only the edge is free, and the organ has a correspondingly smaller range of movement. The FOOD GROOVE is well-developed in A and C, but represented only by a wedge-shaped patch of cilia at the sides of the mouth and a narrow groove along the front quarter of the velum in B. The cilia in the mouth and esophagus are much denser and longer in B. The TENTACLES are well-developed with a prominent eyespot in A, thick and rounded in C, but represented only by an optic vesicle (OV) in B. On the FOOT, the operculum is present, and the statocysts are prominent in A and B. Propodium and metapodium are differentiated and there is a metapodial sensory lobe with bristles in A and C. The propodium is densely covered with large cilia used for turning nurse eggs in C.

Measurements (in μm)

	(VW)	(SL)	(TL)
Thais lamellosa (A)	660	690	750
Thais emarginata (B)	620	720	660
Thais canaliculata (C)	780	660	1000

(VW) – velum width; (SL) – shell length; (TL) – total length

A – anus; AG – anal gland; CG – cerebral ganglion; FB – foot bristles; FCP – frontal ciliary patch; FG – food groove; LH – larval heart; LK – larval kidney; M – mouth; MSL – metapodial sensory lobe; OV – optic vesicle; PCP – post-oral ciliary patch; PRP – pre-oral ciliary patch; S – shell; ST – statocyst; T – tentacle; VC – velar cilia

FEEDING AND DEVELOPMENTAL SEQUENCE

These embryonic feeding mechanisms are operable for only a brief period early in the developmental sequence; the *Thais emarginata* embryos expanded from 290 μm to 1000 μm within 10 days. The older embryos are similar to the free-living veligers, and, like them, are incapable of ingesting large particles.

Older embryos will readily capture small particles available to them with the velar cilia, transport them through the food groove, and ingest them. The major source of particles in a closed capsule is the decomposition of infertile eggs and dead capsule mates. Embryos do not tolerate heating or dehydration, and will be killed if a capsule is exposed directly for a single low tide (SPIGHT, 1972). A few of the embryos from each capsule will die during the 3-month developmental period, and will then decompose and provide food for their living capsule mates.

The feeding of *Thais emarginata* has been described in older works (*e. g.*, JOHNSON & SNOOK, 1927) as "cannibalism." Although some embryos may be consumed by others during the feeding period, all of the encounters we have seen have been peaceful. Older veligers are not capable of killing their fellows and feed on dead fellows only after these decompose to small particles. Feeding on nurse eggs or on dead fellows is "cannibalism" in only the most literal sense. We know of no observations of any muricacean embryos killing their capsule-mates.

EVOLUTIONARY SIGNIFICANCE

Embryos of 5 species have been observed while feeding on nurse eggs, but only 2 of them utilized the same technique. The differences do not correspond with present taxonomic divisions; the 3 members of the subgenus *Nucella* in the group use 3 different means (and the 2 additional Northwest members do not feed on nurse eggs). Mechanisms for feeding on nurse eggs must have evolved independently several times.

The type of embryonic food supply (yolk, nurse eggs, or planktonic algae) used by members of a single species also varies from place to place. Nurse eggs are the major food source for *Thais canaliculata* from California (HOUSTON, 1971), but each egg has its own yolk supply at Friday Harbor. *Thais haemastoma* (Linnaeus, 1758) at some localities feed on nurse eggs and metamorphose in the capsule; at others, all of the eggs are fertile and hatch as free-swimming veligers (THORSON, 1950).

Embryonic food supply is a characteristic that can vary to suit local conditions. The members of the group (Muricacea) are sufficiently variable that it may be possible to determine the precise selective factors that favor planktonic larvae at some localities and direct development at others.

SUMMARY

Muricacean embryos utilize a variety of methods to obtain their yolk supply. Closely related species (*e. g.*, the 4 Northwest *Thais*) may utilize different methods. Geographically separated races of the same species may also utilize different methods; for example, *Thais canaliculata* embryos from California obtain most of their yolk by consuming nurse eggs, while those from Washington do not. Mechanisms for ingesting nurse eggs are operable only during a short period early in the developmental sequence; no older embryos of any species can ingest such large particles.

ACKNOWLEDGMENTS

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NOTE ADDED IN PROOF:

We were unable to find specimens of *Thais canaliculata* at Nick's Cove in June, 1972. HOUSTON's (1971) description of capsules and adults found at this site are compatible with our observations on the *T. emarginata* population there and differ markedly from our observations on *T. canaliculata* in Washington.

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